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THE BIOLOGICAL SIGNIFICANCE OF THE EYE APPENDAGES OF ORGANISMS

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I. INTRODUCTION

The following numbered statements include some of the more important observations which were made use of in formulating the system of thinking submitted in this article. Every outgrowth on the organism which is an obstruction to vision, will be considered an eye appendage; and any other object which serves the same purpose, will be considered a substitute for an eye appendage. For the sake of simplicity, only one or two kinds of animals are referred to in each case. It must always be borne in mind that some of the statements (1-14) are only very general ones; a number of exceptions can be noted in some cases, but a few of the statements scarcely need qualifying.

1) Nocturnal animals have as a rule white whiskers (cats).

2) Those of the diurnal animals are generally dark (squirrels).

3) Animals which are both nocturnal and diurnal have usually some white and some black whiskers; a single whisker may be for half its length black while the other half, the outer half, is white (rabbits).

4) Nocturnal animals which habitually nest in trees have some black and some white whiskers; the black ones project between the eyes and the sky, or the high objects in the trees, while the white whiskers lie between the eyes and the darker objects (in the night they are dark) the animal moves over (many opossums and raccoons).

5) Carnivorous animals possess, as a rule, the most pronounced whiskers.

6) While carnivorous animals lie in wait for prey they close the eyes seldom, but continually move the whiskers (cats owls, etc.).

7) Gregarious birds have usually no whiskers (partridges).

8) Whiskerless birds often nod the head quite periodically (doves, ducks, etc.).

9) Animals with oscelli and compound eyes usually possess prominent antennae which continually move before the eyes (the greater number of the invertebrates).

10) Those invertebrates which have the insect eyes and no prominent antennae, often raise and lower the body spasmodically or else move it from side to side (spiders).

11) As a rule creepers often thrust the tongue out of the mouth (snakes).

12) Many reptiles which lie quiet for long periods of time, often raise and lower the body or nod the head spasmodically (lizards).

13) Many aquatic animals which have no eye appendages frequently rock the body by lifting first one side and then the other (some salamanders such as Megalobatrachus maximus and Cryptobranchus alleghaniensis). Some cave forms have at most very degenerate eyes (Proteus anguinus).

14) Deep sea fishes often possess not only shaky telescoped appendicular eyes (Stylopthalmus paradoxus A. Br.), but some even carry luminous organs (they are supposed to be luminous) on pinnacles near the eyes (Melanocetes krechi A. Br.).

15) When a person carefully fixates with wide-open eyes a small object for only a few seconds, it subjectively disappears; but, as soon as the eyelashes are allowed to fall and for a very short interval of time obstruct the vision, the object reappears. Instead of dropping the lashes, one can cause the object to reappear by allowing a little smoke to pass between the object and the eyes. One can also move the eyes a few mm. to the side. Under any of these conditions the object reappears at once; but it does not necessarily retain its original color. If one carefully fixates a 10 x 10 cm. piece of green paper on a larger gray background, the color of the paper becomes induced on the background, and vice versa, to such an extent that all becomes one solid area of green; one can at times distinguish no transition from the paper to the background. However, if at this stage one lowers the eyelashes, the area of the colored paper becomes at once distinct, even though the color now observed is antagonistic to the previous

one. If one continues to thus move the eyelashes, or sprinkles dust particles over the paper, or spreads a tissue paper over it, or shifts the eyes a few mm. to the side occasionally, or closes the eyelids frequently while fixating, the form of the paper—whatever color it may from time to time assume—is easily retained.

16) If one fixates the green paper with half-closed eyes, it appears reddish after a very few seconds but retains its original form for a long period of time.

The function of eye appendages and their substitutes seems to be to retard the positive or self-induction and to hasten the negative induction of a color. An eye appendage or its substitute which serves this purpose, is a mechanism for training the visual apparatus to respond to colors in quite definite ways, as will be discussed in a later article. I wish now to do no more than merely mention that the organ of vision, including its appendages, is in truth a uniquely devised apparatus for training itself.

To hasten the negative induction of a given color, e. g. green, implies retarding its positive or self-induction, and from the biological standpoint this means of course no more than that a pause for green is hastily brought about. It is a matter of physiological necessity that a pause for green finally comes, simply because the nervous structures which are responsible for the sensation of greenishness cannot function indefinitely. After a recuperation pause for the structures involved, they can re-function and thus produce a second time the sensation of greenishness. If through some mechanical device the pause is hastily brought about, it need not be so long as it otherwise would be; green can be seen much earlier, and of course in a given time it can be seen much oftener. During the recuperation pause the organism is totally but only temporarily color blind for green. If an eye appendage brings about a pause for green before the exhaustion of the nervous structures for this color is very great, the organism will be able to respond sooner and in a given time oftener to the color presented it. The biological significance of this fact should be clear; it means that conditions are produced under which the organism is for no very great length of time blind to the particular color of the surface it fixates.

During the pause for green, I shall call it the 'green-pause,' the organism responds to a color which may be quite different from green; it is usually red, but it is of much greater biological significance that the area remains in one color or another than that it disappears entirely.

Each eyelash, each whisker, each condensed portion of a cloud of smoke, each dust particle, each translucent particle of a tissue paper etc., etc. serves as a background (or a foreground, if one should see fit to call it thus) however small it may be, on which a negative after-effect (in cases a positive after-effect) of the whole or a portion of a larger more distant object can fall either when the eyes move, when the background moves, or when the object behind the little background moves; each of these little backgrounds, whether it be an eye appendage or a substitute for one, produces a pause for a particular area of the retina that has neared exhaustion for green, e. g., but which can function strongly for the most unrelated color to green. Red appears as soon as this exhausted area for green (the exhaustion may be far from being complete) is no longer being directly stimulated by the green. When the nervous structures which terminate in the retina, become in a high degree exhausted for green, which occurs after many seconds of careful fixation, red will appear without the intervention of a background.

Any one of our little backgrounds serves exactly the same purpose for a limited portion of the retina as a large background does for the entire retina. The most natural background for the entire retina is the eyelid which occasionally falls, thus obstructing the vision entirely. If the small backgrounds are plentiful enough they also bring about a pause for the particular color of the fixated object, not necessarily for so many protected parts, but for the entire retina, i. e. for the unprotected areas as well; for the induced color, which makes its appearance under these conditions, can often not be said to be in any way different from that which appears when one closes the lids entirely. One great advantage in having numerous minute backgrounds instead of only one very large one is that the fixation can continue without the point of fixation shifting far or near or to the side; the organism is thereby enabled to see always the object it fixates, even though this object becomes subjectively differently colored.

II. Experiments, Observations, and Discussions

A. The Cat

But what would be the difference for a cat, provided the cat can discriminate between colors, if the mouse's nose it fixates should appear to the cat to be black, white, red, green, yellow or blue? A blue mouse would evidently be better than none. When a cat hears a noise in a pile of boards, it sits quietly near the boards and keeps its eyes turned in the direction of

the noise until the mouse makes its appearance, then the cat usually pounces onto it with one or both paws. If now a mouse comes to the end of a board and exposes only the nose, as mice generally do before scampering out into the open, the cat springs and captures the mouse by scraping it from behind the board with one paw which it can very expertly bend in a sharp angle to fit around the board. If the cat has no whiskers or eyelashes which it can continually move about in its field of vision as it fixates, it should theoretically be often unable to see the nose, because the nose, which is really a small point, should subjectively disappear. The cat must accordingly wait until the mouse shows a larger part of its body or comes entirely from behind the board and skips about. But mice very often show only the nose and turn back. The whiskerless cat would lose these opportunities, which are really good ones for a whiskered cat, and must necessarily live from the mice that venture into the open. Moreover, if a cat fixates an object before it begins to disappear and reappear, it cannot be blamed for growing restless as often as this occurs. And of course, if the cat moves about occasionally, this will disturb the mice. A smaller number of them would then leave their sheltered places to skip about the restless cat.

For many days I observed a cat while it was watching for mice. It evidently lived on mice and rats, for nobody fed it. During one afternoon I saw it catch two mice, and at dusk I found it with a rat. I deprived the cat of its whiskers and again observed it as it watched for mice. I saw it spring several times into the shucks and hay, but it captured no mouse while I was present.[1] It may of course be that I could not so well detect the presence of a mouse as even the whiskerless cat could, but it often seemed to me that the cat sprang when no mouse was about. I supposed that some of the objects which were in the cat's field of vision as it fixated, disappeared, and that when the animal moved its head or partly closed one or the other or both eyes, as it occasionally did, an object that had vanished suddenly reappeared and was mistaken for a mouse, perhaps not for the entire body but for such a small part as the nose.

The cat grew poor, each time it saw me it ran to me, rubbed for a while against my legs, and quite often looked me

[1] I saw it one day with a snow bird that had just been captured, and a few days later I saw it eating a gray squirrel. The squirrel, however, had apparently died from wounds from a shot gun, for I found a number of No. 6 shot in its body. It had been dead so long that its eyes had shrunk.

in the face and meowed. As a whiskered cat it never did this. Instead of feeding it, I glued some rabbit whiskers at various places on its face, as much as possible onto the old whisker stubs. These would move about somewhat as the original whiskers did. For the sake of economy, I tried to give the cat movable whiskers; for a single whisker that moves in the field of vision is certainly worth a number of stationary ones. As long as the false whiskers were intact, the cat behaved just as it originally did; I never observed it spring without catching a mouse. But every time the animal washed its face, the rabbit whiskers would be either badly displaced or scraped entirely away. Since this method caused so much trouble, I shot some horned owls and glued many long shaky pieces of feather down before and behind the cat's eyes. Especially when the ends of these were charged with electricity, which I generated on the cat's back and transferred to the ends of the feathers, they stood out on the face and waved back and forth, in a way resembling the movements of the round arms of a sea anemone. When the cat now washed its face, the down was usually left intact, and all I had to do was to occasionally straighten and recharge the pieces.

I convinced myself that when the cat had false whiskers, it was a much more efficient mouser than when it had none. I saw it catch more mice, and it seemed to get somewhat fatter; but it still remained hungry only for the simple reason that I could not all the while be with it to replace the down it lost, to straighten the pieces that became tangled with the hair, and to keep the ends charged.

I finally captured in a trap another very wild cat which remained in the woods and fields. I shingled its whiskers and eyelashes and set it free. For many days it roamed about as usual, but after about two weeks I often saw it lurking about an old house which had been deserted for more than a year. I never succeeded in getting near enough to the animal to judge whether it was as fat as usual. Through inquiries I learned that the cat belonged to the last family that occupied the house, and that when the animal was deserted it began to roam in the fields and woods. I suppose that it, as a whiskerless cat, became less efficient in catching its prey, finally grew hungry, and returned every now and then to the house where it was formerly well fed.

B. The Squirrel

The squirrel comes onto a branch and carefully fixates another onto which it is preparing to spring. Since the whis-

kers are prominent on the animal's face and since a number of these are directly between the eyes and the branch it fixates, this branch may become white, red, green, blue or any other color (assuming that the squirrel can discriminate between colors). But whatever color it may subjectively become, it still remains for the squirrel a branch to which the animal can respond by springing. If however the branch subjectively disappears, as should occasionally be the case with a whiskerless squirrel, the animal might spring and fall to the ground. With these ideas in mind I captured some squirrels, deprived them of their whiskers, and occasionally set one free. I watched these carefully as they went running and springing through the trees. Very often a squirrel would be in the attitude of springing from the end of a limb of one tree to one of a neighboring tree and after all not spring, but start down the branch it was on, then run back up this branch, fixate the branch of the other tree for a short time, again run down the branch it was on, return again, etc., before it would finally spring. I was quite unable to observe this sort of behavior, which I observed in a limited number of cases, in any marked degree when I chased whiskered squirrels through the woods, or when I remained quiet and observed large colonies of wild squirrels often for four or five hours at a time.

Every one who has given particular attention to squirrels, knows how they jerk the bushy tail when they walk slowly or come to a stand-still. Since this moving tail falls in the animal's field of vision, I thought the hairs on it might possibly play an analogous rôle to that ordinarily played by the whiskers. I therefore sheared the tail of an already whiskerless squirrel and set the animal free. The number of fixations before springing was now unmistakably more, and once the squirrel missed its aim and fell about five feet to some lower branches; later it once fell to the ground.

It can of course be said that the purpose of the squirrel's tail is to guide the body as the animal springs. I have no doubt that this is the case; we might therein find an explanation for the fact that the tailless squirrel missed its branch and fell, but there are in this connection some very important facts to consider.

Following are a few auxiliary observations made on the human being. If one fixates a piece of green paper, e. g., for a very few seconds, and then drops the lashes for a very short distance, however not so far across the field of vision that they come between any part of the paper and the pupil, not only the top part but the whole of it changes immediately to red. So it

seems that since lashes or whiskers that move in any part of the field of vision during the period of fixation, cause the fixated object to remain more distinct, the hairs of a squirrel's tail, which move also in the field of vision, even though behind or above the fixating eyes, would play fundamentally the same rôle. Those hair-like processes, however, which lie directly between the pupil and the object of fixation, whether these be the whisker-like feathers on the sides of an owl's beak, whiskers on the nose of a cat, or lashes on the lids of the human eye, are the more efficient in serving the very important biological purpose of avoiding a subjective disappearance of the object fixated. Even the eyebrows of many human beings (especially among the American Indians) and those of such animals as the eagle, even though these processes come to lie, under conditions, only in the upper region of the field of vision, serve the same purpose. When the eagle or the Indian frowns, as is especially the case when a distant object is being carefully observed, the eyebrows fall and project a short distance into the field of vision just over the eyes; and careful observation shows that they are usually in a perfect tremor. I can observe this best on myself. (I am not a full breed Cherokee, but I nevertheless have many characteristics of this tribe). When I observe a distant object, I involuntarily frown; then the eyebrows nearest my nose project over and before my eyes and quiver. Moreover the skin, which ordinarily lies over the prominent bone projections above and toward the outer corner of each eye, falls at the same time against the eyelashes, thus shoving them over the pupil, though not entirely over it, but usually over only the upper part. Since this skin quivers rapidly, the eyelashes, which it is pushing down, also quiver. The eye of the Indian or of the eagle is, I think, a uniquely efficient apparatus for observing objects at great distances.

It does not matter whether the organism remains quiet as it fixates or whether it moves steadily about from place to place; it may soar in the air or walk steadily over a surface and still lose an object it fixates. When the surface is more or less homogeneous, such as is the case when a snow is on the ground, the fixated objects disappear more readily. While I was in the Ozarks, during the months of November, December, 1915, and the greater part of January 1916, hunting and performing the experiments already mentioned in this paper, I often found it necessary to walk a few miles to my hunting grounds. I followed the railroad track and learned to walk a rail for the entire distance without falling. Often after I had walked a mile or two, the track subjectively dis-

appeared, but returned again as soon as I puffed some smoke, not necessarily between the track and my eyes, but merely formed a smoke cloud at some place in the field of vision, or frowned, or reached my hand out before my eyes merely so that I could view it peripherally, or merely glanced at some distant object. At other times the track did not entirely disappear; when this was the case the parts between the ties remained quite normal while the other parts seemed to dip and pass under each tie. It was necessary for me to walk very steadily and at the same time fixate the track. My fixating the track as I walked steadily over it was analogous to my standing still and fixating a limited portion of it; under this condition it also disappeared for me. This was especially true at dusk, for the track, which was then for me much more like its surroundings, disappeared much more readily than in the day time.

When the rail apparently dipped under the ties, each tie was of course subjectively continuous where it was previously cut by the darker rail; each tie that crossed my field of vision induced itself across the darker rail. I observed in each case no more than an induced positive color (I use the Ladd-Franklin terminology and call everything colors excepting the psychological absolute black which I will define in a later article) of the tie and indeed an effect of long duration; for when I stood still I could often observe the induced color for a minute or more, i. e. until the entire tie disappeared, or, until I made a sudden movement of any kind, lowered the eyelashes, frowned, or did anything else of similar nature. In connection with this, I found it interesting to stand on the small railroad bridges (where the ties are much closer together than ordinarily) and fixate a tie and observe it as it suddenly flowed, as it were, to the neighboring ties, which in turn seemed to flow into the next ones, etc., until all became one homogeneous surface. I could easily avoid this illusion by throwing, among other things, the lashes over my eyes. It certainly did me no harm to have this illusion. If I had taken a step forward to walk to the other end of the bridge, the chances are that I would have stepped on a tie, for the simple reason that they were only about six inches apart; however, if my feet had been quite small I could possibly have stepped between two ties. If I had taken a step to walk to the other side of the bridge, i. e. across to the other rail, the chances for my falling would have been greater.

I can avoid the simultaneous positive induction of the color of the ties very easily by moving my hand in my field of peri-

pheral vision; I need not bring the hand between my eyes and the ties. It would seem that it is just as unnecessary for the squirrel's tail to fall directly between the animal's eyes and the branch it fixates. The jerking tail serves a distinct biological purpose even though it never falls directly between the eyes and the objects before the squirrel. We must furthermore consider that the squirrel often sits on its haunches and brings the tail up over its back. When it sits thus the tail is more directly in the field of vision, and this should really be the case; for the eyes are now in such a position that the squirrel can observe objects back of it almost as well as before it.

C. The Rabbit

The rabbit certainly needs no whiskers while running, for it does not move steadily over the earth, but leaps and bounds. Since the animal lies roughly entrenched, in a high degree unsheltered, during the day in open fields and with its head motionless and close to the ground, it needs black whiskers which project between the eyes and the sky, or in other words between the eyes and its diurnal enemies. Such whiskers are really present and they are constantly moving. The rabbit, which is by nature nocturnally inclined, is compelled by its many diurnal enemies to be more or less passively diurnal itself.

The rabbit would need no whiskers in the night time provided it never stopped running, but since it does stop and moreover since it often sits on its haunches, it really does need some. Furthermore, since it runs in the *evening* and at *night,* it needs some *white* ones. A white whisker on a dark background is of course more effective than a black whisker would be. When the animal is in the sitting posture, its head is quite differently inclined than while it is running or lying. The nose is now considerably higher than the eyes and consequently, owing to this position of the head, the white ends of some long half black and half white whiskers, which are rooted so low down under the nose that they serve the animal no purpose as it lies in its bed, now fall between the eyes and the dark objects on the earth. It is also interesting that the outer or white ends of these whiskers fall between the eyes and the more distant objects while the inner or black ends obstruct the vision for the closer ones. The black diurnal whiskers are thus converted into nocturnal ones by being thrown between the eyes and the horizon; and the white or nocturnal ones, which were of no use to the animal during the day, now lie in the most favorable possible position. This arrangement of the whiskers

of the sitting fixating rabbit enables it, among other things, to observe carefully its many nocturnal enemies. Besides its whiskers, its long moving ears also play a prominent rôle as eye appendages; the ears would seem to render a long bushy rabbit tail a nuisance as an eye appendage.

D. The Opossum

The opossum sleeps soundly during the day in secluded places, usually in tree cavities or in deserted nests of other arboreal animals. In the night time the animal walks or trots *steadily* over the earth. It should therefore have two sets of whiskers, some white ones which fall between the eyes and the dark objects it moves over, and some black ones which lie between the eyes and the higher objects which are surrounded by the light sky.

III. Conclusion

Paradoxical as it may sound, it seems that appendages on the body and substitutes for these which are really physical obstructions in vision, may after all have the very important biological significance of enabling the organism to retain objects it fixates. Since the carnivorous animals must necessarily fixate very often and for exceptionally long periods of time, it is not strange that they possess the most elaborate eye appendages. The herbivorous animals do not need to fixate so carefully the herbs they live on, but the significance of the occasionally highly developed eye appendages is nevertheless often to be understood when one carefully studies the activities of these animals. It is moreover not strange that animals which possess neither a great number of these appendages nor even a few moving ones, should very often spasmodically move the head or the entire body. Animals which live in flocks have a sufficient number of substitutes for eye appendages at their disposal. For any one of these animals, other members of the flock play the part of moving eye appendages. This is only one example of innumerable substitutes for eye appendages.